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Spiders in wheat: First quantitative data for North America

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Abstract. Spiders were sampled quantitatively, by vacuum insect net (D-vac) followed by hand search, in Russian wheat aphid-resistant and -susceptible cultivars of winter wheat in Colorado. Spider densities were unaffected by cultivar, aphid density or wheat tiller density. Compared to other parts of the world, spider densities were one to two orders of magnitude lower, and the fauna more evenly dispersed over families rather than being dominated by the Linyphiidae. Given their very low densities, unmanipulated spider populations may be incapable of exerting significant biological control on cereal aphids in this system. Habitat manipulations such as those that have increased spider populations in wheat in Europe are under investigation.

Key words: Aphididae, Araneae, cereals, *Diuraphis noxia*, Linyphiidae, tritrophic interactions

Introduction

Chemical insecticides are relied upon almost exclusively for cereal aphid control in the US Great Plains. In 1993–1994 for example, $1.2 million in insecticides was applied to control the greenbug, *Schizaphis graminum* (Rondani), and $9.5 million to control the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Webster and Amosson, 1995; Webster and Treat, 1996). However, exclusive reliance on chemical insecticides is problematic for several reasons: (1) *S. graminum* has the potential to become insecticide-resistant (Teetes et al., 1975; Shufran et al., 1996; Rider et al., 1998); (2) in many parts of the Great Plains, small grain production is so marginal economically that insecticide purchase and application costs are difficult for many growers to justify (Duff et al., 1995; Webster and Amosson, 1995); (3) insecticides reduce aphid natural enemy populations (Basedow et al., 1985; Matcham and Hawkes, 1985), and may thereby exacerbate pest management problems; (4) the public is concerned about environmental contamination

(Daily et al., 1998), including effects on wildlife (Grue et al., 1988; Flickinger et al., 1991).

Such concerns have sparked a renewed commitment to the adoption of integrated pest management (IPM) programs in US Agriculture. Though IPM may, by definition, include the use of pesticides (Kogan, 1998), sustainability of cereal production systems will require a reduction in insecticide use and concomitant increased reliance on other IPM components. The other key components of sustainable cereal IPM programs for the foreseeable future are resistant cultivars, modified tillage regimes, and biological control by arthropod natural enemies (Burton et al., 1987; Reed et al., 1991; Rice and Wilde, 1991; Farid et al., 1997; 1998; Brewer et al., 1998).

The natural enemies of cereal aphids comprise specialized parasitoids and oligophagous and polyphagous predators. The parasitoids are well known (Kring and Gilstrap, 1983; Elliott et al., 1992, 1994; Michels and Whitaker-Deerberg, 1993; Bernal et al., 1997; Pike et al., 1999). Some groups of predators in cereals are known in broad outline, but most of our detailed knowledge is from the Palearctic (Sunderland et al., 1987; Nyffeler and Benz, 1988; Riedel, 1991, 1995; Booij et al., 1995; De Snoo et al., 1995; Samu et al., 1996; Petersen, 1999). There is a significant literature on Carabidae in cereals in North America (Allen, 1979; Elliott et al., 1998; French et al., 1998; French and Elliott, 1999), but information on other groups is fragmentary (Rice and Wilde, 1991; Elliott et al., 1998); with one exception (Doane and Dondale, 1979), investigations on spiders are completely lacking from the North American wheat predator literature.

This principal goal of this study was to determine the diversity and density of spiders in a typical US Great Plains winter wheat growing situation. Preliminary data were also gathered on the questions of whether maintenance of spider populations is compatible with the deployment of an aphid-resistant wheat cultivar, whether spiders aggregate at aphid infestations, and whether spiders respond to plant density.

Materials and methods

Study site and experimental design. The experiment, a randomized complete block design with repeated measures, was performed near the town of Lamar in Prowers Co., Colorado (102°73′W, 38°06′N), an area subject to infestations of *D. noxia*. There were two blocks, on each of two quarter sections (64.8 ha) located 2.1 km apart. Each block comprised two adjacent 1 ha plots of hard red winter wheat (*Triticum aestivum* L.), the first of the *D. noxia*-resistant cultivar ‘Halt’ (Quick et al., 1996), and the other of the susceptible cultivar ‘TAM 107’ (Porter et al., 1987), which is widely planted in the region (Figure

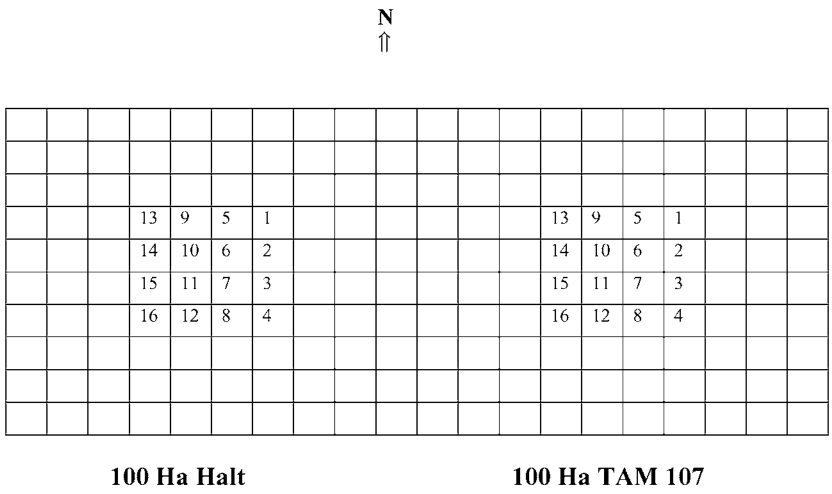

Figure 1. Layout of one block of the experiment.

1). The blocks were situated ⩾ 25 m from the field edge; the remaining area of each quarter section was planted to TAM 107. Wheat was drilled into the previous year's sorghum stubble in a sorghum-wheat-fallow rotation. It was planted the week of 12 September 1996 and harvested 25 June 1997. The blocks were not sprayed with pesticides during the course of the experiment.

Sampling. Only the central 40 m × 40 m square of each 1 ha plot was sampled. Stakes were placed every 10 m around and through the sample area, to define sixteen subplots of 100 m^2 each (Figure 1). Plots were sampled twice-monthly from 6 October 1996 to 17 June 1997, with a break from mid-November to mid-March when arthropod densities are usually low. The two plots of each block were sampled between 0800 and 1200 on one of two consecutive days, in order to reduce possible effects of time-of-day on spider catchability (Lowrie, 1971). On each date, 12 of the 16 candidate subplots were chosen from a random number table. Within each of these 12 subplots, one of the 100 possible 1-m^2 sample points was chosen at random.

Sampling is diagrammed in Figure 2. After visually identifying the sample point, the investigator threw a 20 cm deep, 0.5 m^2 circular toothed sampling frame over the wheat and forced the teeth of the frame into the soil to block the escape of spiders. The enclosed area was sampled with a D-vac® (D-vac Co., Ventura, CA, USA) fitted with a ventilated 60 cm long cylindrical sheet-metal extension to prevent crushing of the spiders against the plants. The frame was then intensively searched for additional spiders. Juvenile and

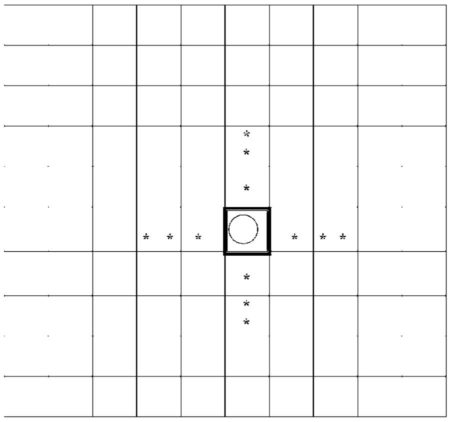

Figure 2. Diagram of sampling protocol for one subplot. Each square is 1 m × 1 m; the sampling frame is situated within the randomly selected 1 m^2 sample point.
○ = 0.5m^2 sampling frame; * = Tiller collection point.

foliage-inhabiting spiders are more efficiently sampled by D-vac, while adults and ground dwellers are more efficiently sampled by hand search (Sunderland and Topping, 1995). Spiders collected during the ground search were placed immediately into 70% EtOH; D-vac bags were maintained in a cooler until they could be returned to the laboratory for processing.

Aphid densities were estimated by counts on tillers (Elliott et al., 1990; see Lersten, 1987 for description of wheat morphology). Twelve tillers – three in each of the cardinal compass directions – were collected at distances of two, three and four paces from the sampling frame (Figure 2), and placed in plastic bags that were returned to the laboratory in the cooler. Tiller density was determined by counting the number along a 1 m length of row adjacent to the sampling frame and multiplying by the number of rows/m.

Voucher specimens of spiders have been deposited at the California Academy of Sciences.

Analysis. To test for treatment and date effects, the spider and aphid density data were square root-transformed and subjected to PROC MIXED in PC SAS Version 6.11 (SAS Institute, 1996). When a significant interaction in treatment by date was detected, the simple effects of treatment were analysed given date. Fisher exact tests (two-tailed) of contingency tables in SAS PROC FREQ were used to determine whether spiders responded to aphid and plant densities.

Results

Phenology

Spiders were present during the entire experiment, sparsely from October through early May and greatly increasing over the last three sampling periods (Table 1). The most abundant family was the Linyphiidae, with almost one-quarter of all individuals. The Lycosidae had 14% of individuals, followed by about 10% each for the Thomisidae, Gnaphosidae, Tetragnathidae, and Theridiidae. Identities of those animals that could be identified to genus or lower are given in Table 2; all other individuals were immatures or were otherwise unable to be determined more precisely.

Aphid occurrence is shown in Table 3. *Rhopalosiphum maidis* (Fitch) was found only during the first three sampling periods, and always in relatively low numbers. *Diuraphis noxia* appeared on 2 April and remained in relatively low numbers until June, when it increased markedly. *Rhopalosiphum padi* (L.) was found sporadically, in low numbers, throughout the duration of the experiment. No aphids were found during the 19–20 March sampling interval.

Treatment effects

The distribution of animals across treatments, blocks and dates is shown for spiders in Table 4 and for aphids in Table 5. The ANOVAs show a significant effect of date for spiders, and significant effects of date, and treatment X date interaction, for aphids (Tables 6A and 6B). Analysis of the simple effects of treatment given date indicates that for spiders these effects were due to the absence of spiders in the Halt plots on 19 October and 22 April (Tables 4 and 7A); for aphids they were due to the majority of *D. noxia* being in the TAM plots on 6 May, 21 May, and 4 June (Tables 5 and 7B).

Associations between spider, aphid, and tiller densities

Because of discontinuities in the distribution of spider densities (Table 4), the data did not lend themselves well to analyses of correlations with aphid and tiller densities. Therefore the presence or absence of spiders was tested for association with three density classes of aphids: none, 1–99/m^2, and $\geqslant$ 100/m^2; and three density classes of tillers: $\leqslant$ 300/m^2, 301–500/m^2 and >500/m^2. Two-tailed probabilities from Fisher exact tests on these data, presented in Table 8, suggest that spiders do not tend to aggregate in areas of high aphid density, and tend not to respond to tiller density.

Table 1. Spider individuals per family, per 6 m^2, on each sample date

Starting date	Aran	Dict	Gnap	Liny	Lyco	Oxyo	Phil	Salt	Tetr	Ther	Thom	Totals
6 Oct 96			2		1							3
19 Oct 96		1	2		1					1		5
2 Nov 96			2		3							5
19 Mar 97	1		3				1					5
2 Apr 97			2		1							3
22 Apr 97	2	1		1	2					3		9
6 May 97		1		2	1							4
21 May 97	2	7	5	8	10	1		1	1	4	4	43
4 Jun 97	8	1	1	24	4			3	4	7	8	60
17 Jun 97	3	1	1	4	1			1	10		8	29
Totals	16	12	18	39	24	1	1	5	15	15	20	166
Proportion	0.10	0.07	0.11	0.23	0.14	0.01	0.01	0.03	0.09	0.09	0.12	1.0

Aran = Araneidae, Dict = Dictynidae, Gnap = Gnaphosidae, Liny = Linyphiidae, Lyco = Lycosidae, Oxyo = Oxyopidae, Phil = Philodromidae, Salt = Salticidae, Tetr = Tetragnathidae, Ther = Theridiidae, Thom = Thomisidae

Table 2. Identifiable spider taxa collected

Family	Species
Dictynidae	*Emblyna consulta* (Gertsch and Ivie)
Gnaphosidae	*Gnaphosa clara* (Keyserling)
	Haplodrassus eunis Chamberlin
	Haplodrassus sp.
Linyphiidae	*Meioneta sima* (Chamberlin and Ivie)
	Tennesseellum formicum (Emerton)
Philodromidae	*Ebo* sp.
	Tibellus sp.
Salticidae	*Euophrys diminuta* (Banks)
	Habronattus altanus (Gertsch)
Theridiidae	*Steatoda albomaculata* (DeGeer)
	Theridion rabuni Chamberlin and Ivie
Thomisidae	*Misumenops celer* (Hentz)
	Misumenops coloradensis Gertsch

Table 3. Aphid individuals per species, per 144 tillers, on each sample date

Starting date	*R. maidis*	*R. padi*	*D. noxia*	Totals
6 Oct 96	33	5		38
19 Oct 96	32			32
2 Nov 96	96	19		115
19 Mar 97				0
2 Apr 97			15	15
22 Apr 97		11	38	49
6 May 97			27	27
21 May 97			50	50
4 Jun 97		6	785	791
17 Jun 97			442	442
Totals	161	41	1357	1559

Table 4. Spider individuals per treatment plot, per 6 m^2, on each sample date, in wheat cultivars resistant (Halt) and susceptible (Tam 107) to *Diuraphis noxia*

Starting date	Halt I	Halt II	Tam 107 I	Tam 107 II	Totals
6 Oct 96	1	1	1		3
19 Oct 96			3	2	5
2 Nov 96	1			4	5
19 Mar 97	3	1	1		5
2 Apr 97	1		1	1	3
22 Apr 97			2	7	9
6 May 97	2		1	1	4
21 May 97	4	24	4	11	43
4 Jun 97	16	19	7	18	60
17 Jun 97	2	11	5	11	29
Totals	30	56	25	55	166

Table 5. Aphid individuals per treatment plot, per 144 tillers, on each sample date; Halt I is resistant, and Tam 107 susceptible, to *Diuraphis noxia*

Starting date	Halt I	Halt II	Tam 107 I	Tam 107 II	Totals
6 Oct 96	2	18	7	11	38
19 Oct 96	3	7	7	15	32
2 Nov 96	30	41	11	33	115
19 Mar 97					0
2 Apr 97			15		15
22 Apr 97		16	27	6	49
6 May 97			24	3	27
21 May 97			45	5	50
4 Jun 97	42	35	464	250	791
17 Jun 97	126	84	95	137	442
Totals	203	201	695	460	1559

Table 6A. Results of spider ANOVA; treatments are wheat cultivars resistant (Halt) and susceptible (Tam 107) to *Diuraphis noxia*.

Source	df	SS	MS	F	$P > F$
Block	1	0.88	0.88	2.31	0.3703
Treatment	1	0.58	0.58	1.54	0.4320
Block × Treatment	1	0.38	0.38		
Date	9	48.28	5.36	7.09	0.0002
Treatment × Date	9	8.93	0.99	1.31	0.2970

Table 6B. Results of aphid ANOVA; treatments as in Table 6A.

Source	df	SS	MS	F	$P > F$
Block	1	1.47	1.47	0.15	0.7644
Treatment	1	59.38	59.38	6.09	0.2451
Block × Treatment	1	9.75	9.75		
Date	9	608.06	67.56	23.19	0.0001
Treatment × Date	9	137.81	15.31	5.25	0.0014

Table 7. Spider and aphid treatment effects given date; treatments are wheat cultivars resistant (Halt) and susceptible (Tam 107) to *Diuraphis noxia*; df = 1 in all cases

	A. Spiders				B. Aphids			
Starting date	SS	MS	F	$P > F$	SS	MS	F	$P > F$
6 Oct 96	0.25	0.25	0.33	0.33	0.02	0.02	0.01	0.9297
19 Oct 96	2.47	2.47	3.27	3.27	1.15	1.15	0.39	0.5385
2 Nov 96	0.25	0.25	0.33	0.33	1.99	1.99	0.68	0.4198
19 Mar 97	0.75	0.75	0.99	0.99				
2 Apr 97	0.25	0.25	0.33	0.33	3.75	3.75	1.29	0.2715
22 Apr 97	4.12	4.12	5.45	5.45	3.32	3.32	1.14	0.2997
6 May 97	0.09	0.09	0.11	0.11	10.99	10.99	3.77	0.0679
21 May 97	0.63	0.63	0.83	0.83	20.00	20.00	6.86	0.0174
4 Jun 97	0.54	0.54	0.71	0.71	155.69	155.69	53.43	0.0001
17 Jun 97	0.17	0.17	0.22	0.22	0.28	0.28	0.10	0.7595

Table 8. Results of Fisher exact tests (two-tailed probabilities) on spider presence and aphid densities, and spider presence and tiller densities; aphids were absent on 19 March 1997, and only one tiller density category was occupied on 6 October 1996

Starting date	Spider presence and aphid densities	Spider presence and tiller densities
	P	*P*
6 Oct 96	1.000	
19 Oct 96	0.197	1.000
2 Nov 96	0.816	0.635
19 Mar 97		0.126
2 Apr 97	1.000	0.052
22 Apr 97	0.258	0.650
6 May 97	1.000	1.000
21 May 97	0.511	0.895
4 Jun 97	0.088	0.256
17 Jun 97	0.159	0.192

Discussion

Most studies of spiders in wheat, including the only other North American one (Doane and Dondale, 1979), used pitfalls for sampling. Two published quantitative studies that used sampling technology identical to this one (Sunderland, 1987; Topping and Lövei, 1997) reveal that in Colorado the evenness component of diversity is much greater, and total densities are much lower, than in some other parts of the World. While linyphiids make up only 23% of individuals in Colorado, they completely dominate winter wheat in the UK, with 71–100% of all individuals (Sunderland, 1987), and in New Zealand, with 100% of all individuals (Topping and Lövei, 1997). Total spider density in Colorado averaged 0.7/m^2, compared with 12.5–103.1/m^2 (UK), and 1.8/m^2 (New Zealand). Working in Switzerland, Jmhasly and Nentwig (1995) employed suction sampling without a following hand search, and used a machine of a different design. If we assume that their machine had a similar sampling efficiency, and given the absence of a hand search, their density estimate of 10.1/m^2 may be an underestimate.

Another striking aspect of these data is the relatively low species richness, especially compared with Europe: 39 species in Switzerland (Jmhasly and Nentwig, 1995), 43 in Spain (Castañera and del Estal, 1985), 101 in Germany (Basedow, 1998), 104 in France (Cocquempot and Chambon, 1989), 149 in

Hungary (Tóth and Kiss, 1999), and 151 in the UK (Sunderland, 1987). Of these, only the study of Jmhasly and Nentwig (1995) is at all comparable to the present one, having been performed by suction sampling with hand search (added for species richness but not density determination) for a single field season. The others all employed pitfall trapping and, with one exception (Castañera and del Estal, 1985), encompassed several seasons and sometimes several fields or farms (Sunderland, 1987; Cocquempot and Chambon, 1989; Basedow, 1998). Hence the greater number of species recorded in those studies may simply reflect the power of accumulated sampling, especially of transient species, over space and time. Alternatively they may reflect real differences, possibly caused by the greater landscape diversity, due to smaller fields, more crop types, and greater use of hedgerows and other bordering vegetation, in Europe compared with the US Great Plains.

Since my data only encompass one field season, it is possible that the unusual pattern described here is not typical for the Great Plains. However, samples collected in another year (spring of 1999) at another Great Plains site reveal similar dominance-diversity patterns and densities. Approximately 450 km ESE of Lamar, near the town of Lahoma in Major Co., Oklahoma (98°08′W, 36°25′N), tetragnathids and linyphiids dominated the fauna, with about 38 and 36% of individuals respectively, while seven other families each made up fewer than 6% of the individuals; the mean density, $2.7/m^2$, while slightly higher than in Lamar, was of the same order of magnitude (unpublished data). Continuing sampling will reveal whether these provisional patterns are representative of Great Plains wheat.

Failure of spiders to track aphid densities is not surprising given the aphids' patchiness and biotic potential. Their failure to track tiller density is somewhat surprising given the influence of vegetation structure on spider density and diversity in other systems (Lubin, 1978; Abraham, 1983; Rypstra, 1983; Greenstone, 1984). Apparently, differences in tiller density do not create structural heterogeneity sufficient to influence species density or species richness. Since all wheat fields appear to be quite similar structurally, differences in structural diversity cannot explain the differences in dominance and density of linyphiids in Colorado, the UK and New Zealand.

Salient differences between wheat fields in Colorado and the other localities are climate, landscape features, and geographical accidents. The climate of southeastern Colorado, like that of much of the Great Plains, is notable for its aridity. It seems reasonable that linyphiids, by virtue of their small size, would be especially susceptible to desiccation, and hence disadvantaged under such climatic conditions. However, Almquist (1971) found that the susceptibility of spiders, including linyphiids, to desiccation is independent of size, and some of the smallest linyphiids in his study exhibited survival rates as good as those of larger spiders. Relatively low densities in New Zealand, which has the highest rainfall of the three sites, also argue against the desiccation hypothesis. On the other hand arthropod predator densities may tend to be generally low in New Zealand (Sunderland, et al., 1995; Lövei and Cartellieri, in press).

Linyphiid population dynamics in relation to landscape features have been modeled by Topping (1997, 1999). His conclusions suggest that larger fields, as in Colorado, tend to lead to larger, not smaller, populations, but that the extent and timing of mortality (Topping, 1997), and of dispersal (Topping, 1999) may also be influential. A major determinant of mortality is the timing and intensity of cultural practices (Topping, 1997), another set of variables that may differ among the UK, New Zealand and Colorado sites.

One of the biggest accidents of geography may be the absence from the Great Plains of *Lepthyphantes tenuis* Blackwall, the linyphiid that dominates wheat fields in the UK, Western Europe and New Zealand. This single species may just happen to be exquisitely adapted to wheat fields, and there may be no ecologically equivalent linyphiid in the Great Plains. Also in the category of geographical accidents is the spider species assemblage available to colonize wheat fields from adjacent habitats, which may comprise more robust competitors of linyphiids than those in the Old World and New Zealand. Until more wheat fields, and the natural ecosystems in which they are embedded, are quantitatively sampled, the causes of low linyphiid density and diversity in southeastern Colorado wheat fields will remain a mystery.

Given their very low densities in Colorado wheat fields, unmanipulated spider populations may be incapable of exerting significant biological control on cereal aphids in this system. Employment of a simple habitat modification that can raise spider densities many-fold, viz., provisioning web sites by placing holes in the soil (Alderweireldt, 1994; Samu et al., 1996), is the subject of an ongoing investigation.

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